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STHENURUS BAILEYI SP. NOV., A NEW FOSSIL KANGAROO FROM THE PLEISTOCENE OF SOUTHERN AUSTRALIA

by GAVIN J. PRIDEAUX* & RODERICK T. WELLS*

Summary

PRIDEAUX, G. J. & WELLS, R. T. (1998) *Sthenurus baileyi* sp. nov., a new fossil kangaroo from the Pleistocene of southern Australia. *Trans. R. Soc. S. Aust.* **122** (1), 1-15, 29 May, 1998.

Sthenurus baileyi sp. nov. is described from Pleistocene deposits of Eyre Peninsula and the southeast of South Australia. The dentary is similar in size and morphology to *S. occidentalis* Glauert, 1910 but the cranium is much less inflated across the frontals and the rostrum less tapered anteriorly. *Sthenurus baileyi* is characterised by very low crowned molars, most similar to *S. cegsai* Pledge, 1992. *S. brachyselenis* Prideaux & Wells, 1997 and *S. antiquus* Bartholomai, 1963. Upper and lower premolars are similar to *S. antiquus* and *S. brownei* Merrilees, 1967. Overall, *S. baileyi* appears most closely related to *S. antiquus* and may represent the most plesiomorphic member of the lineage containing the more brachycephalic sthenurine species.

KEY WORDS: *Sthenurus baileyi* sp. nov., *Sthenurus antiquus*, *Sthenurus*, *Simosthenurus*, sthenurine kangaroo, Victoria Fossil Cave, Naracoorte, Brothers Islands, Eyre Peninsula, Pleistocene.

Introduction

Following its discovery in 1969, the extensive Pleistocene deposit within Victoria Fossil Cave at Naracoorte, South Australia has yielded remains from around one hundred vertebrate species. Included are slightly less than half of the known Pleistocene species of sthenurine kangaroos (subfamily Sthenurinae): *Procoptodon rapha* Owen, 1874, *Sthenurus andersoni* Marcus, 1962, *S. brownei* Merrilees, 1967, *S. gilli* Merrilees, 1965, *S. maddocki* Wells & Murray, 1979, *S. occidentalis* Glauert, 1910, *S. pales* DeVis, 1895 (Wells *et al.* 1984), and a new sthenurine, *S. baileyi* sp. nov. The species is also known from a single specimen collected from an eroded cave on one of the Brothers Islands in Coffin Bay, Eyre Peninsula (Brown 1908; Fig. 1). Williams (1980) identified the cranium and associated dentaries as *Sthenurus* cf. *maddocki*, but it is here designated as the holotype of *S. baileyi* sp. nov. Description of the new species and a consideration of its phylogenetic implications form the subject of this paper.

Materials and Methods

The material is housed in the South Australian Museum, Adelaide (prefix SAMA) and Flinders University (prefix FU). Dental homology follows Flower (1867) and Luckett (1993). Dental nomenclature follows Tedford & Woodburne (1987), Ride (1993) or is standard. Mensuration follows Tedford (1966) and Wells & Murray (1979). Dental measurements (mm) are provided in Table 1.

Fig. 1. Map of southeastern Australia showing location of deposits yielding *Sthenurus baileyi* sp. nov.

Systematics

Order Diprotodontia Owen, 1866
Suborder Phalangerida Aplin & Archer, 1987
Superfamily Macropodoidea (Gray, 1821)
Family Macropodidae Gray, 1821
Subfamily Sthenurinae (Glauert, 1926)
Genus *Sthenurus* Owen, 1874
Subgenus *?Simosthenurus* Tedford, 1966

Sthenurus (?Simosthenurus) baileyi sp. nov. (FIGS 1-8)

Holotype: SAMA P13670, partial cranium (with I1-3, dP2, dP3, M1-4, excavated P3; Fig. 2A,B, 3A, 4A,

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TABLE 1. *Cheek tooth dimensions of* Sthenurus baileyi, S. brachyselenis, S. brownei *(eastern form)*, S. cegsai *and* S.antiquus: *mean, standard deviation (parentheses), range (brackets).*

Abbreviations: L = length, AW = width of anterior loph(id); PW = width of posterior loph(id); AH = crown height of anterior loph(id) on buccal side; PH = crown height of posterior loph(id) on buccal side; n = sample size. Note that crown heights are heavily dependent on degree of enamel wear, hence, frequently high standard deviations.

Tooth	Species	L	AW	PW	AH	PH	n
UPPER DENTITION							
dP2	*S. baileyi*	10.5	7.5	10.0	6.2	6.1	1
	S. baileyi TYPE	As above					
	S. brownei (eastern form)	10.9 (0.43) [10.4-11.9]	8.7 (0.40) [8.1-9.5]	10.8 (0.38) [10.4-11.4]	7.0 (0.51) [6.0-8.0]	7.9 (0.60) [6.6-8.7]	15
S. cegsai	-	-	-	-	-	-	
	S. antiquus	-	-	-	-	-	-
dP3	*S. baileyi*	10.6	9.9	10.8	-	-	1
	S. baileyi TYPE	As above					
	S. brownei (eastern form)	11.3 (0.29) [10.6-11.7]	10.7 (0.32) [10.2-11.3]	11.0 (0.37) [10.6-11.8]	5.7 (0.54) [4.8-6.4]	5.9 (0.46) [5.3-6.8]	15
	S. cegsai	9.3	8.6	9.2	6.3	6.3	1
	S. antiquus	-	-	-	-	-	-
P3	*S. baileyi*	17.2 (0.14) [171.-17.3]	9.9 (0.28) [9.7-10.1]	12.9 (0.21) [12.7 13.0]	9.8 (0.28) [9.6-10.0]	9.7 (1.06) [8.9-10.4]	2
	S. baileyi TYPE	17.1	10.1	13.0	10.0	10.4	
	S. brownei (eastern form)	17.1 (0.57) [16.2-18.0]	10.9 (0.68) [9.0 11.8]	13.7 (0.81) [12.1-15.0]	9.8 (0.76) [8.3-11.1]	9.7 (0.78) [8.6-11.3]	21
	S. cegsai	-	-	-	-	-	-
	S. antiquus	14.9	8.3	11.3	8.4	10.1	1
M1	*S. baileyi*	12.3 (0.14) [12.2-12.4]	12.3 (0.21) [12.1-12.4]	12.3 (0.21) [12.1-12.4]	6.3 (0.07) [6.2-6.3]	6.6 (0.42) [6.3-6.9]	2
	S. baileyi TYPE	12.2	12.1	12.1	6.2	6.3	
	S. brownei (eastern form)	12.9 (0.43) [12.2-13.6]	12.4 (0.40) [11.6-13.0]	12.3 (0.34) [11.8-13.1]	6.1 (0.76) [5.0-7.9]	6.5 (0.62) [5.3-8.1]	28
	S. cegsai	-	-	-	-	-	
	S. antiquus	12.4	12.0	12.1	-	-	1
M2	*S. baileyi*	13.8 (0.21) [13.6-13.9]	13.2 (0.21) [13.0-13.3]	13.1 (0.14) [13.0-13.2]	6.9 (0.42) [6.6-7.2]	7.2 (0.35) [6.9-7.4]	2
	S. baileyi TYPE	13.6	13.3	13.0	7.2	7.1	
	S. brownei (eastern form)	14.1 (0.37) [13.2-14.7]	13.6 (0.46) [12.9-14.4]	13.1 (0.43) [12.5-14.3]	6.6 (0.76) [5.3-7.8]	6.9 (0.58) [5.8-8.0]	23
	S. cegsai	-	-	-	-	5.6	1
	S. antiquus	14.9 (0.07) [14.8-14.9]	13.4 (0.14) [13.3-13.5]	13.0 (0.21) [12.8-13.1]	7.2 (1.13) [6.4-8.0]	7.4 (1.34) [6.4-8.3]	2
M3	*S. baileyi*	14.5 (0.00) [14.5]	13.7 (0.21) [13.5-13.8]	12.6 (0.35) [12.8-13.3]	7.0 (0.14) [6.9-7.1]	6.8 (0.28) [6.6-7.0]	2
	S. baileyi TYPE	14.5	13.5	12.8	7.1	6.6	
	S. brownei (eastern form)	14.5 (0.39) [13.7-15.5]	14.0 (0.50) [13.3-14.8]	12.9 (0.54) [12.3-14.5]	6.7 (0.62) [5.4-8.1]	7.0 (0.53) [5.9-8.1]	19
	S. cegsai	13.1 (0.07) [13.0-13.1]	11.5	10.9 (0.14) [10.8-11.0]	5.4 (0.00) [5.4]	5.5 (0.14) [5.4-5.6]	2
	S. antiquus	16.0 (0.35) [15.7 16.2]	13.6 (0.49) [13.2-13.9]	12.9 (0.85) [12.3-13.5]	8.3 (0.35) [8.0-8.5]	8.3 (0.00) [8.5]	2
M4	*S. baileyi*	13.8	13.4	11.3	6.7	6.1	1
	S. baileyi TYPE	As above					
	S. brownei (eastern form)	14.0 (0.43) [13.2-14.5]	12.2 (0.48) [11.3-13.0]	11.2 (0.40) [10.6-12.0]	8.1 (0.62) [7.4-9.6]	7.4 (0.78) [6.5-8.8]	16
	S. cegsai	12.2	11.0	9.5	5.5	5.1	1
	S. antiquus	-	-	-	-	-	

TABLE 1. – Continued

LOWER DENTITION							
dp2	*S. baileyi*	9.6	7.5	8.9 (0.99) [8.2-9.6]	7.3	6.2 (0.71) [5.7-6.7]	2
	S. baileyi TYPE	9.6	7.5	8.2	7.3	5.7	
	S. brachyselenis	8.1	5.1	6.1	5.7	5.5	1
	S. brownei (eastern form)	9.8 (0.45) [9.2-10.9]	6.5 (0.34) [5.9-7.2]	9.1 (0.36) [8.6-9.7]	7.5 (0.82) [5.8-8.7]	7.1 (0.71) [6.0-8.2]	17
	S. cegsai	-	-	-	-	-	-
	S. antiquus	-	-	-	-	-	-
dp3	*S. baileyi*	9.8 (0.14) [9.7-9.9]	8.9 (0.71) [8.4-9.4]	9.1 (0.28) [8.9-9.3]	6.0	6.0	2
	S. baileyi TYPE	9.9	8.4	8.9	-	-	
	S. brachyselenis	10.2	7.8	8.2	6.2	7.0	1
	S. brownei (eastern form)	10.4 (0.36) [10.0-11.1]	9.2 (0.46) [8.4-10.0]	9.3 (0.31) [8.7-9.8]	7.3 (0.47) [6.6-8.2]	7.2 (0.63) [6.0-8.2]	17
	S. cegsai	-	-	-	-	-	-
	S. antiquus	-	-	-	-	-	-
p3	*S. baileyi*	16.2 (0.78) [15.3-17.8]	8.0 (0.32) [7.7-8.4]	9.7 (0.44) [9.1-10.3]	9.5 (1.04) [7.9-11.0]	9.0 (1.03 [7.3-10.2]	6)
	S. baileyi TYPE	15.3	7.9	9.5	8.9	9.0	
	S. brachyselenis	13.8	6.3	8.0	7.3	6.7	1
	S. brownei (eastern form)	16.2 (0.53) [15.2-17.0]	8.5 (0.34) [8.0-9.5]	10.3 (0.58) [9.4-11.5]	9.9 (0.85) [8.9-11.4]	9.9 (0.83) [8.9-11.3]	19
	S. cegsai	14.8	6.5	7.2	8.3	7.1	1
	S. antiquus	17.6	8.2	10.1	12.2	11.4	1
m1	*S. baileyi*	12.0 (0.41) [11.5-12.5]	10.1 (0.22) [9.9-10.4]	10.1 (0.26) [9.8-10.4]	7.1 (1.01) [6.3-8.5]	7.0 (0.76) [6.3-8.0]	4
	S. baileyi TYPE	12.1	10.0	10.2	6.4	6.5	
	S. brachyselenis	13.9	9.9	10.3	9.3	9.4	1
	S. brownei (eastern form)	13.1 (0.64) [12.1-14.7]	10.4 (0.49) [9.4-12.0]	10.6 (0.43) [9.6-11.5]	8.6 (1.04) [6.4-10.0]	8.7 (1.07) [6.5-10.2]	29
	S. cegsai	10.5	-	-	-	-	1
	S. antiquus	13.8	-	11.0	8.5	8.5	1
m2	*S. baileyi*	13.3 (0.46) [12.8-13.9]	11.4 (0.27) [11.0-11.6]	11.2 (0.41) [10.7-11.7]	8.3 (0.49) [7.8-8.9]	8.4 (0.63) [7.8-9.2]	4
	S. baileyi TYPE	12.8	11.5	11.7	8.0	8.0	
	S. brachyselenis	-	-	-	-	-	-
	S. brownei (eastern form)	14.7 (0.53) [13.8-16.1]	11.4 (0.39) [10.4-12.0]	11.7 (0.33) [11.1-12.2]	9.5 (0.94) [8.2-10.8]	9.5 (0.80) [8.0-11.2]	21
	S. cegsai	12.7	10.8	10.3	5.9	5.9	1
	S. antiquus	15.3 (0.85) [14.7-15.9]	11.9 (0.71) [11.4-12.4]	12.1 (0.78) [11.5-12.6]	10.4	10.4	2
m3	*S. baileyi*	14.1 (0.64) [13.6-15.0]	12.2 (0.37) [11.7-12.6]	11.9 (0.42) [11.4-12.4]	8.2 (0.93) [7.0-8.9]	7.9 (0.71) [6.9-8.4]	4
	S. baileyi TYPE	13.6	12.6	12.4	7.8	7.8	
	S. brachyselenis	-	-	-	-	-	-
	S. brownei (eastern form)	14.9 (0.51) [13.7-15.7]	12.0 (0.43) [11.2-12.9]	12.2 (0.35) [11.4-12.9]	9.3 (0.61) [8.4-10.3]	9.1 (0.73) [7.5-10.4]	21
	S. cegsai	12.8	11.0	10.2	7.0	6.4	1
	S. antiquus	16.0 (0.99) [15.3-16.7]	12.4 (0.42) [12.1-12.7]	12.2 (0.49) [11.8-12.5]	10.5	10.3	2
m4	*S. baileyi*	13.9 (0.11) [13.7-14.0]	12.1 (0.26) [11.8-12.3]	11.1 (0.42) [10.5-11.5]	7.4 (0.43) [7.1-8.0]	7.2 (0.35) [6.9-7.8]	5
	S. baileyi TYPE	13.8	12.2	11.2	7.1	7.1	
	S. brachyselenis	-	-	-	-	-	-
	S. brownei (eastern form)	14.0 (0.43) [13.2-14.5]	12.2 (0.48) [11.3-13.0]	11.2 (0.40) [10.6-12.0]	8.1 (0.62) [7.4-9.6]	7.4 (0.78) [6.5-8.8]	16
	S. cegsai	11.9	10.3	8.6	5.3	5.3	1
	S. antiquus	15.4 (0.49) [15.0-15.7]	12.4 (0.21) [12.2-12.5]	11.0	8.5 (0.35) [8.2-8.7]	7.7 (0.35) [7.4-7.9]	2

5A), left and right dentaries (with i1, dp2, dp3, m1-4, excavated p3; Fig. 3B, 4B, 5C,D), apparently collected from a bone breccia in an eroded cave on the western end of west Brothers Island (34° 35' S, 135° 20' E), Coffin Bay, Eyre Peninsula South Australia (Brown 1908; Williams 1980; Fig. 1). Other mammals from the deposit include *Macropus rufogriseus*, *Potorous platyops*, *Pseudocheirus* sp., *Rattus fuscipes* and *Neophoca cinerea*. A large bird femur previously attributed to *Genyornis newtoni* (Rich 1979) belongs to *Dromaius novaehollandiae* (J. McNamara pers. comm. 1996). Age of type locality is considered Pleistocene because all taxa identified to species are only known from the Quaternary. Similarly, the genus *Sthenurus* appears not to have existed anywhere beyond the late Pleistocene. Details of collection are uncertain but probably retrieved by D. R. George around 1902 (J. McNamara pers. comm. 1996).

Diagnosis

Cranium similar in size to *Sthenurus occidentalis* but frontals less expanded, rostrum shorter and broader, with wider nasals and larger narial aperture. P3 similar to *S. browni* but with relatively narrow, shallow longitudinal basin and two accessory cuspules anterior to prominent posterobuccal accessory cusp. Upper molars very low crowned, with short precingulum, weak postprotocrista and very well developed postparacrista. Dentary similar in size and morphology to *S. occidentalis* and *S. antiquus* Bartholomai, 1963 but with more posteriorly inflated pterygoid fossa than in any *Sthenurus* species. Posteroventral border of masseteric fossa expanded laterally into wide shelf, similar to *S. cegsai*, *S. gilli* and *S. maldocki*. i1 intermediate between *S. occidentalis* and *S. browni* in general shape and degree of procumbency. p3 most similar in morphology to *S. antiquus* but lower crowned, with straighter lingual crest. Lower molars very low crowned, with anteroposteriorly short trigonid, well-developed premetacristid, and very reduced cristid obliqua and paracristid producing a morphology closest to *S. cegsai*, *S. antiquus* and *S. brachyselenis* Prideaux & Wells, 1997 but wider relative to length.

Description of holotype

Vertical portion of premaxilla flared dorsally providing elongate contact with nasals. Diastema short, anterior ⅓ comprising premaxilla and posterior ⅔ maxilla. Incisive foramina long, narrow, anterior border level with posterior extreme of I3 alveolus (Fig. 3A). Rostrum short, tapered anteriorly (Fig. 2A). Buccinator fossa on maxilla rather shallow anteriorly, deeper posteriorly anterior to zygomatic arch. Masseteric process well-formed, rather narrow, eroded off ventrally on left and right sides. Nasals very broad posteriorly and, although broken anteriorly, clearly short. Nasofrontal suture gently sinusoidal (Fig. 2A). Frontals moderately inflated anteriorly; supraorbital crests only slightly developed (Fig. 2A). Temporal crests moderately developed, not fully convergent upon sagittal suture. Large infraorbital foramen positioned anteroventral and mesial to lachrymal foramen, just below orbital centre. Palatal vacuities extend anteriorly to anterior extreme of M1 (Fig. 3A). Right lateral extremity of broken postpalatine bar level with M4 interloph valley.

I1 crown rather long, moderately wide, with vertical occlusal surface facing posteriorly. I2 very small, splint-like, ⅓ size of I1. I3 high crowned, but quite short anteroposteriorly (Fig. 2B). Small anterolingual lobe evident on I3.

dP2 reminiscent of P3, rounded in general outline, especially lingually, but much shorter relative to width (Fig. 4A). Buccal and lingual crests straight, except for buccal curvature of lingual crest at posterior extremity. Anterior basin small, quite deep and separated from longitudinal basin by low transverse ridgelet. Posterior basin appears to have been relatively large, approx. half size of longitudinal basin.

dP3 completely molariform and similar in general outline to M1, but differs by having lophs orientated obliquely (not perpendicular) to buccal and lingual sides of tooth (Fig. 4A). In addition, precingulum very slight terminating before reaching lingual extreme of tooth. Premetacrista appears well-developed. Protoloph appears to have been very curved, convex anteriorly. No enamel crenulations present in interloph valley; very low, barely detectable postprotocrista positioned just lingual of dP3 midline (Fig. 4A). Postmetaconulecrista curves dorsobuccally from metaconule to meet vertical postmetacrista. Small accessory crest positioned mesial to postmetacrista, slight postlink centrally positioned on posterior metaloph face.

P3 rounded in outline and tapered anteriorly (Fig. 5A). Longitudinal basin shallow. Buccal crest barely exceeding lingual crest in height. Anteriorly, lingual crest begins to run parallel to buccal crest then posterior ⅔ of crest curves out lingually. Small anterior basin present and separated from longitudinal basin by transverse ridge descending from anterior buccal cusp terminating adjacent to anterior lingual cusp. Posterior basin short, well-formed and separated from longitudinal basin by low transverse ridge originating from posterior lingual cusp and orientated obliquely (slightly anterobuccally) to meet low down on buccal crest. Main posterobuccal accessory cusp well-formed, not quite as high as posterior part of buccal crest. Three

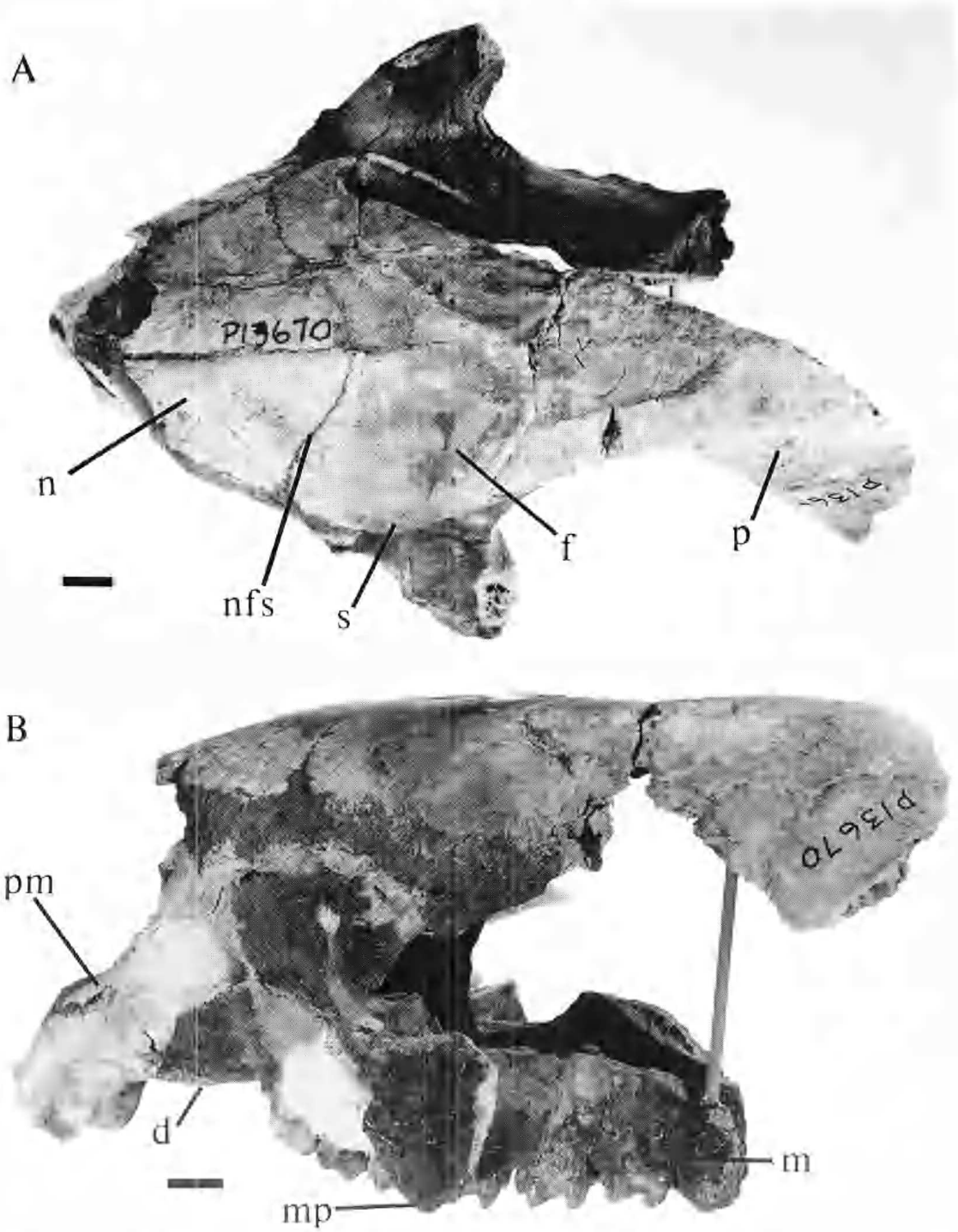

Fig. 2. *Sthenurus bailevi* sp. nov. cranium. A. Holotype (P13670) dorsal view. B. Holotype lateral view. Scale bars = 10 mm. Abbrevs: d = diastema, f = frontal, m = maxilla, mp = masseteric process, n = nasal, nfs = nasofrontal suture, p = parietal, pm = premaxilla, s = supraorbital crest.

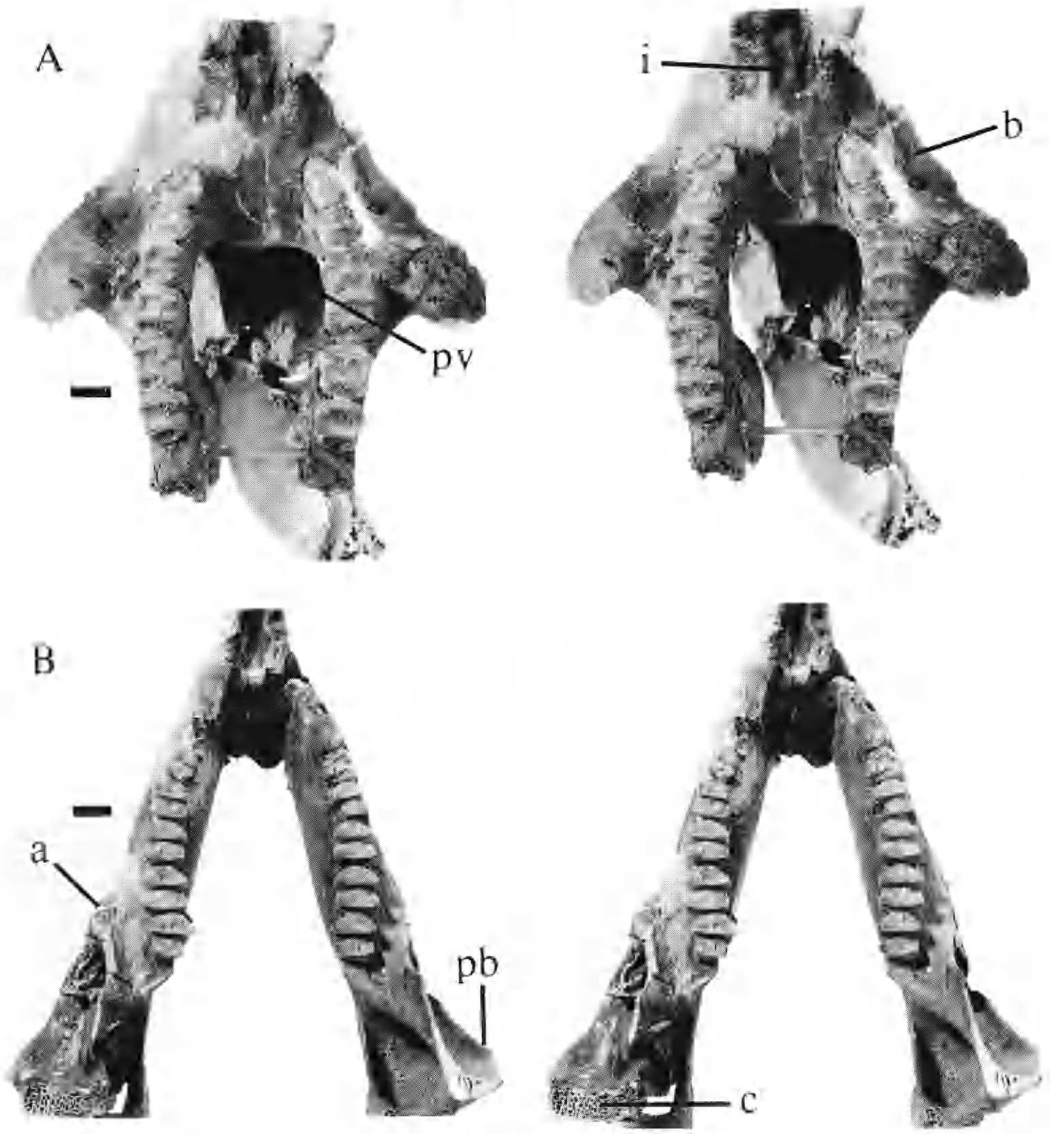

Fig. 3. *Sthenurus baileyi* sp. nov. cranium and dentaries. A. Stereopair of holotype cranium (P13670) palatal view. B. Stereopair of holotype dentary occlusal view. Scale bars = 10 mm. Abbrevs: a = anterior root of ascending ramus, b = buccinator fossa on maxilla, c = mandibular condyle, i = incisive foramina, pb = posteroventral border of masseteric fossa, pv = palatal vacuities.

small poorly separated accessory cuspules positioned anterior to main accessory cusp (Fig. 5A).

Upper molars very low crowned, with protoloph equal in width to metaloph in M1-2, but wider in M3-4 (Fig. 4A). Precingulum short, buccal extreme terminating at distinct cuspule, representing either stylar cusp A or B. Slight crest (probable paracrista) connects cuspule posteriorly to paracone. Two to four slight vertical crenulations centrally located on precingulum, with most lingual probably remnant preprotocrista (forelink). Postprotocrista weak, low, ascending buccally across face of protoloph into interloph valley, uniting with vertical crenulation directed posteriorly from mid-point on protoloph. Postparacrista strongly developed, forming buccal border of interloph valley, meeting slight premetacrista on anterior face of metaloph (Fig. 4A). Interloph valley with few very fine to no enamel crenulations. Postmetaconulecrista sweeps across posterior face of metaloph terminating just posterior to end of postmetacrista. Two to three small distinct crenulations enclosed by postmetaconulecrista on metaloph posterior face.

Dentary moderately proportioned, except for

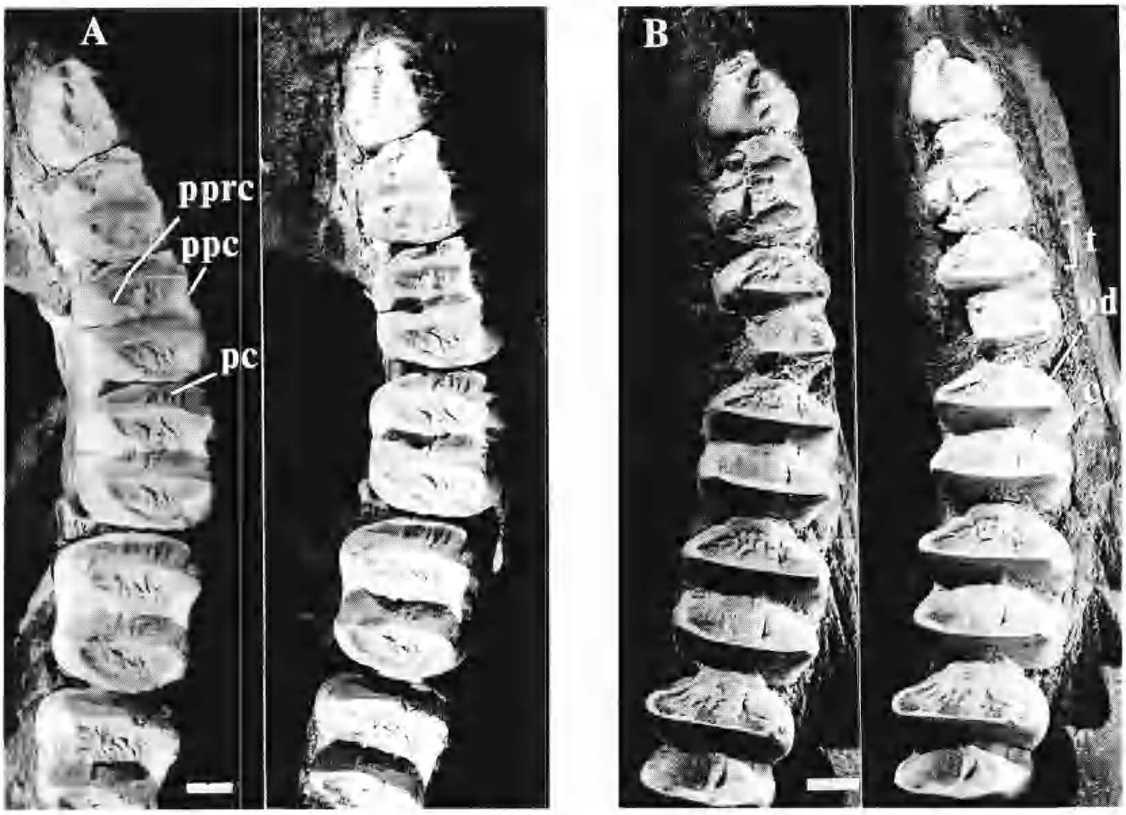

Fig. 4. *Sthenurus baileyi* sp. nov. cheek tooth rows. A. Stereopair of holotype (P13670) left upper cheek tooth row occlusal view. B. Stereopair of holotype (P13670) right lower cheek tooth row occlusal view. Scale bars = 5 mm. Abbrevs: co = cristid obliqua, pc = precingulum, pd = paracristid, ppc = postparacrista, pprc = postprotocrista, t = trigonid.

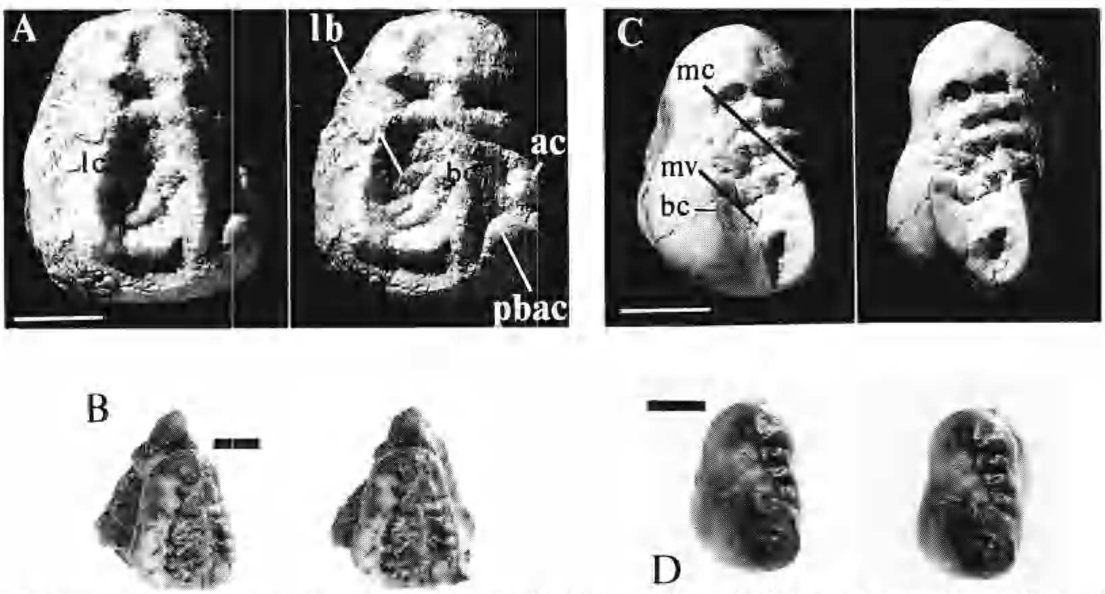

Fig 5. *Sthenurus baileyi* sp. nov. premolars. A. Stereopair of holotype (P13670) left P3 close-up occlusal view. B. Stereopair of paratype (FU0167) left P3 occlusal view. C. Stereopair of holotype left p3 close-up occlusal view. D. Stereopair of holotype left p3 occlusal view. Scale bars = 5 mm. Abbrevs: ac = accessory cuspules, bc = buccal crest, lb = longitudinal basin, lc = lingual crest, mc = main crest, mv = median valley, pbac = posterobuccal accessory cusp.

posteriorly inflated pterygoid fossa and lateral expansion of posteroventral border of masseteric fossa into wide shelf. Ramus moderately deep for width, particularly in region of symphysis. Symphysis gently tapered anteriorly and posteriorly, only extended short way beneath genial pit, below anterior root of dp3. Digastric eminence present but not particularly prominent. Digastric sulcus extending from below anterior extreme of pterygoid fossa to below m2 hypolophid. Diastema short, with median dorsal groove deep, relatively wide. Very shallow buccinator sulcus arises near posterior extreme of diastema, dorsal to large anterior mental foramen. Buccinator sulcus deepens slightly posteriorly, terminates below m1 hypolophid. Posterior mental foramen positioned below m2 hypolophid, half-way between dorsal and ventral borders of ramus.

Anterior root of ascending ramus begins adjacent to m3 hypolophid (Fig. 3B), extending posteriorly to form buccal border of postalveolar fossa. Pterygoid fossa inflated posteriorly, projecting well beyond border of masseteric fossa when viewed laterally. Masseteric fossa deep, due largely to laterally expanded posteroventral border (Fig. 3B). Ventral border of masseteric fossa at same horizontal level as posterior region of buccinator sulcus. Masseteric foramen moderately large, vertical in orientation. Inferior mandibular foramen rather small. At anterior extreme of pterygoid fossa, anteromedial to inferior mandibular foramen, dorsoventrally wide mylohyoid groove present. This appears to have been partially overhung by sharp anterodorsally-directed process at anteromedial border of pterygoid fossa, and similarly-shaped posteroventrally-directed process positioned below posterior extreme of postalveolar fossa. Mandibular condyle moderately large (Fig. 3B). Angular process well-developed, rising dorsally to acute point.

i1 rather short, slender, upturned, with occlusal surface at a horizontal level just above base of cheek teeth crowns. dp2 on both sides of holotype too worn or fragmentary to interpret. Likewise, dp3 very worn, although clearly molariform, possessing low but well-defined para-, premeta-, prehypo- and preento-cristids.

p3 considerably longer than any molar, with main (lingual) crest extending from posterolingual corner to midline of tooth anteriorly (Fig. 5C,D). Three cuspules form anterior part of main crest, with each bearing pair of lateral ridgelets, one descending buccally, one lingually. Buccal ridgelets terminate at low shelf formed by three confluent cuspules, located immediately anterior to buccal crest. Buccal crest straight, short, equal in length to and mirroring shape of posterior part of main crest. Median valley rather narrow, moderately deep. Toward its posterior 1/3, median valley traversed by coarse ridgelet (Fig. 5C,D).

Lower molars very low crowned, with protolophid and hypolophid occlusal surfaces linear and close to parallel. Trigonid very short, with paracristid low and composed of two moieties. Degree of separation of anterior and posterior moieties increases from m1 to m4. Posterior part of paracristid sweeps smoothly anterolingually across protolophid face, terminates on buccal side of anterior part. In more posterior molars, anterior component of paracristid shifted more lingually but posterior extreme remains within buccal 1/3 of anterior protolophid face, originating well below lophid apex. A few fine enamel crenulations arise low down on anterior face of protolophid and descend into trigonid basin. Lingual side of trigonid bordered by well-developed premetacristid, which terminates at paraconid. Precingulid small and positioned anterobuccal to paracristid, extending lingually as very thin peninsula at anterior extreme of molar. Cristid obliqua (prehypocristid) low, similarly developed and aligned in similar position on hypolophid as paracristid on protolophid. Preentocristid very low and barely detectable. Aside from these weakly developed crests, shallow interlophid valley bears no enamel crenulations. Posterior face of hypolophid with low, shallow inflation.

Paratypes: From Victoria Fossil Cave, Naracoorte, South Australia (37° 00' S, 140° 48' E): FU0004, left and right adult dentaries; FU0167, left P3, M1 (P3 in Fig. 5B); FU0168, right p3; FU0294, partial right dentary; SAMA P16531/P16558, left and right adult dentaries (left dentary in Fig. 6A,B); P28282, right juvenile dentary; P28659, right M2, left M3. FU0004, FU0167 and SAMA P28659 may belong to same individual based on proximity in deposit, degree of enamel wear and occlusal fit. Specimens collected by Prideaux, Wells and others. Age of deposit is medial to late Pleistocene (Wells *et al.* 1984; Ayliffe *et al.* in press).

Features not preserved adequately in holotype are described from paratype SAMA P28282.

dp2 equal in length to dp3, very similar in morphology to p3 but wider relative to length. As in p3, three cuspules dominate anterior half of main crest, each with transverse ridgelet on buccal side. Ridgelets likely to have terminated in tiny cuspules like p3, but due to considerable wear sustained have become confluent with buccal crest, conveying an impression of more elongate crest.

Completely molariform, dp3 bears protolophid tapered more toward lophid apex than hypolophid. As with dp2, wear has removed several features. However, cristid obliqua appears more strongly developed than in molars and curved directly from hypoconid apex into interlophid valley, terminating

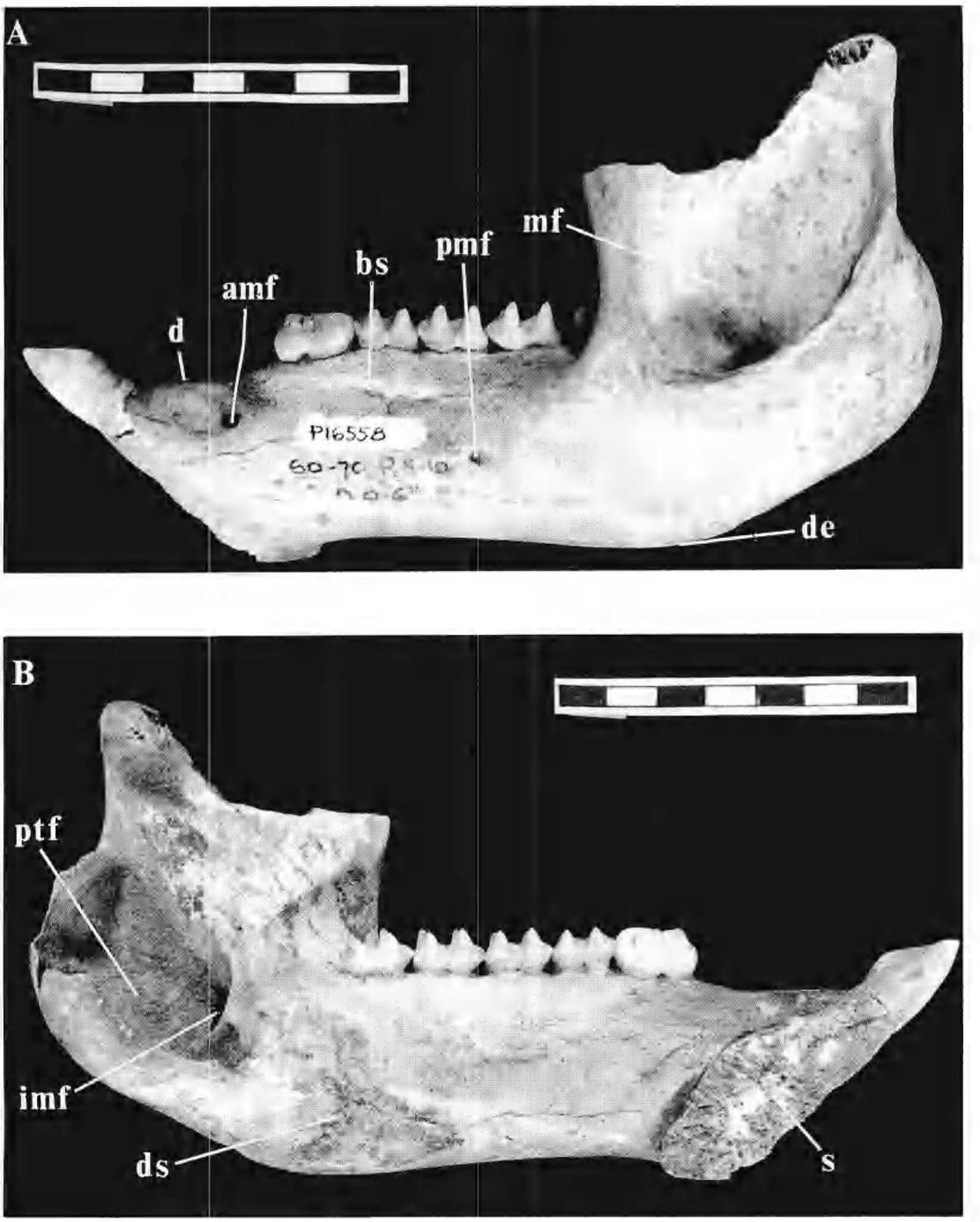

Fig. 6. *Sthenurus baileyi* sp. nov. left dentary. A. Paratype (P16558) lateral view. B. Paratype (P16558) mesial view. Scale bars = 70 mm. Abbrevs: amf = anterior mental foramen, bs = buccinator fossa, d = diastema, de = digastric eminence, ds = digastric sulcus, imf = inferior mandibular foramen, mf = masseteric fossa, pmf = posterior mental foramen, ptf = pterygoid fossa, s = symphysis.

centrally on posterior protolophid face. Very weak precentocristid also present, curving from entoconid into interlophid valley, terminating lingual to cristid obliqua. Enamel crenulations, similar to those on molars, appear to have been present on anterior lophid faces. Slight, rounded postcingulid on posterior face of hypolophid appears confluent with slight postentocristid.

Etymology

Named in honour of Mr Edwin "Ed" Bailey whose efforts over the last 25 years have contributed so much to the success of palaeontological work in the Naracoorte Caves.

Variation

Unfortunately, only one cranium is known of *S. baileyi* sp. nov. and variation within the upper dentition can only be assessed by comparison of P3 and M1-3, which are each represented by two specimens. P3 is very similar in the holotype and FU0167, with the slight occlusal wear in FU0167 responsible for most of the superficial differences between the specimens. In the holotype, P3 is slightly wider anteriorly, both across the whole tooth and the longitudinal basin. The lingual surface of the holotype P3 is slightly more convex and rounded than FU0167. The three cuspules anterior to the main posterobuccal accessory cusp are more separated in FU0167.

Only one slight difference is detectable on comparison of M1-3 of P13670, FU0167 (M1) and P28659 (M2-3). The postparacrista is larger in the holotype. While greater wear sustained by FU0167 and P28659 could account for these differences, consideration of the manner in which teeth occlude suggests that they are more likely to reflect morphological variation.

Complete or partial denturies are known for five individuals, with three characters clearly variable. Depth and extent of the digastric sulcus is the most variable character. Although deep and extending from the anterior extreme of the pterygoid fossa to below the m2 hypolophid in P13670 and P16531/P16558, the sulcus is much shallower and only extends to below the m4 protolophid in FU0004. In P28282, the digastric sulcus is even shallower, thus negating the diagnostic utility of this character. The degree to which the pterygoid fossa is inflated posteriorly also varies between specimens. Inflation is greatest in P16531/P16558, slightly less in the holotype (P13670), FU0004 and P28282, and least in FU0294. However, it is sufficient in the latter to mark it as a distinctive feature of *S. baileyi*. Dentary depth relative to width is greater in P16531/P16558 (depth to width ratio below m2-3 = 1.79) compared to FU0004 (1.65) and P28282 (1.61). The ratio is lowest in the holotype (1.46). Intraspecific variation in dentary depth relative to width is commonly observed in sthenurine species known from even small sample sizes.

Variation in p3 size is common in all sthenurines, including *S. baileyi*. While most of the paratypes are very similar in size, P16530/P16551 and the holotype are noticeably shorter and narrower. Morphology varies only slightly between individuals, primarily in the form of the buccal crest and minor variation in width of the median valley. The anterior half of the buccal crest in P28282 is slightly higher than the posterior half and curves posterolingually, becoming confluent with a transverse ridgelet which crosses the median valley. This buccal crest morphology is not observed in any of the other specimens, although a very similar transverse ridgelet traverses the median valley in P13670. Apart from this feature, only the relative inflation of the anterior region of the p3 varies slightly. A p3 referrable to *S. baileyi* is also known from Lindsay Hall Cave, near Madura on the Nullarbor Plain, Western Australia but this specimen remains in the private collection of L. Hatcher, Perth. This specimen is inseparable in size and morphology from the South Australian specimens.

There is little variation in both size and morphology of the lower molars, although the premetacristid, paracristid and cristid obliqua of the paratypes are slightly more weakly developed than the holotype and the anterior lophid faces bear more fine enamel crenulations. In addition, the postcingulid is more shelf-like in each of the paratypes than in the holotype, except in FU0294 where there is a larger inflation of the ventrobuccal region of the hypolophid posterior face.

Comparison with other taxa

Cranium. Although P3 was unerupted in the holotype of *S. baileyi* sp. nov., the presence of M4 in occlusion indicates that P3 eruption was imminent. An examination of other species for which a good age series is known, reveals that little change in morphology or size in most aspects of the cranium and dentary occurs from this ontogenetic stage to the stage where P3 is erupted. This means that direct comparisons with older representatives of other taxa are tenable. It is worth noting that the two samples of *S. brownei* and *S. occidentalis* with which *S. baileyi* is compared come from Naracoorte and are considered to represent the eastern forms of both species. Although very similar in overall morphology, they can be distinguished from the topotypic Western Australian samples by their larger overall size and slightly smaller dentition relative to jaw size.

The cranium of *S. baileyi* is very similar in size and brachycephaly to *S. occidentalis*. The premaxillae are also similar in relative size and morphology. Although rostral length of the two species is similar, the buccinator fossa on the side of the maxilla is deeper in *S. occidentalis*. This is coupled with a mesially concave aspect to the edge of the diastema, in contrast to the less distinct edge and shallow buccinator fossa in *S. baileyi*. This condition is more reminiscent of *S. gilli* and *S. andersoni*.

The rostrum of *S. baileyi* does not taper to the same degree anteriorly as *S. occidentalis*, both because the frontals are less expanded and its narial aperture is proportionally larger. Among the *Sthenurus* species for which the splanchnocranium is known, lateral inflation of the frontal region (particularly anteriorly) and formation of supraorbital crests is greatest in *S. maddocki*, *S. occidentalis*, *S. stirlingi* Wells & Tedford, 1995 and *S. brownei*. The frontal region is relatively narrow in *S. gilli*, *S. andersoni* and *S. tindalei* Tedford, 1966. The proportions displayed in *S. baileyi* are intermediate between these two groups, particularly between *S. brownei* and *S. gilli*. However, the nasals of *S. baileyi* are very wide and constitute a greater proportion of the dorsal aspect of the rostrum than any other *Sthenurus* species, except *S. maddocki*. Overall, the short and broad nature of the rostrum is characteristic of *S. baileyi*.

The anterior extent of the palatal vacuities in *S. baileyi* is akin to a number of other species, terminating close to the dP3 metaloph, or what would be close to the posterior extreme of the P3 if it were in occlusion. The masseteric process appears to have been well-developed, allowing for the damage in the holotype, and is intermediate between *S. maddocki* and *S. brownei* in size.

Upper Dentition. In *S. baileyi* sp. nov., the crown of I1 is slightly longer and broader than *S. brownei* and is most similar to *S. occidentalis*. It is not as high crowned as that of *S. gilli*, and not as broad as in *S. andersoni*, *S. atlas* (Owen, 1838), *S. tindalei* or *S. pales*. The small, cylindrical I2 is intermediate in size between *S. brownei* and *S. occidentalis*. I3 is most similar in size and general morphology to *S. brownei* but the buccal surface is smooth and flat, not bearing any vertically-orientated undulations. In this respect, *S. baileyi* is similar to *S. occidentalis* and *S. gilli*.

Although slightly shorter and less inflated laterally than in *S. brownei*, dP2 of *S. baileyi* sp. nov. is closest in overall morphology to that species. Orientation of the buccal and lingual crests is also similar but the posterior basin appears to have been larger in *S. baileyi*. P3 of *S. baileyi* is most reminiscent of *S. brownei* and *S. antiquus* in morphology, particularly in the shape and orientation of the buccal and lingual crests and the anterior basin (Fig. 7). However, *S. baileyi* possesses a shallower and narrower longitudinal basin and a prominent posterobuccal accessory cusp with two cuspules anterior to it (Fig. 7). The posterior basin is smaller than in either *S. antiquus* or *S. brownei*. Height of the lingual crest in *S. antiquus* is considerably lower relative to the buccal crest than in either *S. brownei* or *S. baileyi*. In addition, the *S. antiquus* P3 is also smaller relative to the size of the molars. The amount of wear that dP3 has undergone has obliterated several characters useful for comparison. However, the tooth appears to have been generally similar to that of *S. brownei* but with a smaller precingulum, larger premetacrista and many fewer and finer enamel crenulations on the loph faces and interloph valley.

The very low crowned nature of the *S. baileyi* upper molars is only approached among *Sthenurus*, by *S. cegsai*, *S. antiquus* and *S. maddocki*. Similar to *S. cegsai* and *S. antiquus*, there are few crenulations on the loph faces and the interloph valley but the postprotocrista is more weakly developed in *S. baileyi*. The postparacrista is more strongly

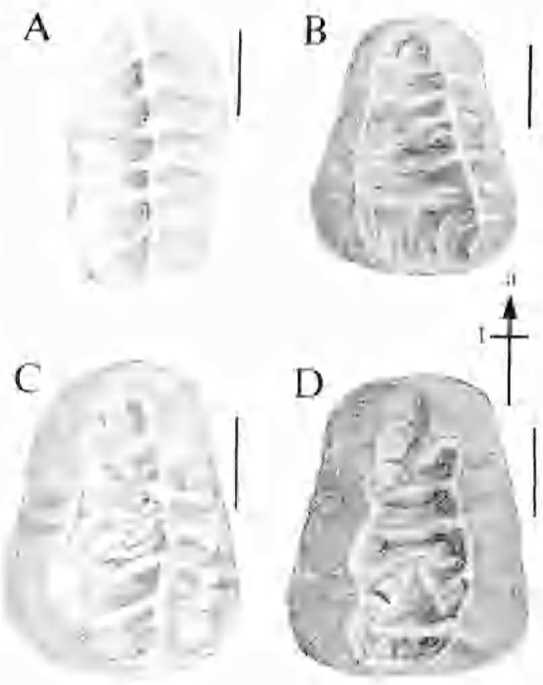

Fig. 7. Comparative sketches of left P3 in occlusal view. A. *Hadronomas puckridgi*. B. *Sthenurus antiquus* (posterolingual corner reconstructed – incomplete in actual specimen). C. *S. baileyi* sp. nov. D. *S. brownei*. Scale bars = 5 mm. Abbrevs: a = anterior, l = lingual.

developed in *S. baileyi* than any other species, including *S. brownei*. The slight nature of the precingulum is similar to that of *S. antiquus*.

Dentary. In general morphology, the dentary of *S. baileyi* sp. nov. is most similar to *S. occidentalis*, *S. antiquus* and *S. gilli*, and to the former two in size. The ramus differs from *S. occidentalis* in the following features: it is slightly narrower for its depth, the symphysis extends only just beneath the genial pit, the i1 and symphysis are slightly more procumbent, the diastema is slightly longer, the digastric sulcus is shallower and less extensive, the posteroventral border of the masseteric fossa is more flared laterally and the pterygoid fossa is more inflated posteriorly. *Sthenurus baileyi* differs from *S. antiquus* in its longer cheek tooth row relative to ramus depth. Morphology of the *S. baileyi* symphysis most resembles that of *S. maddocki*, where the symphysis tapers gently anteriorly and only extends slightly below the genial pit. However, unlike *S. maddocki*, the orientation of i1 closely approximates that of the anteroventral border of the symphysis and in this respect is similar to *S. occidentalis* and *S. brownei*. Morphology of the i1 crown and its degree of procumbency are intermediate between *S. occidentalis* and *S. brownei*. Relative to the length of the ramus, the diastema of *S. baileyi* is proportionally longer than that of *S. occidentalis*, *S. brownei* and *S. gilli*. It is most similar in length to *S. maddocki* but is not convex dorsally as in this species. Depth and extent of the digastric sulcus are similar to, but slightly more pronounced than in *S. maddocki*. The degree of intraspecific variation in depth and extent of the digastric sulcus also seems similar between the two species. Lateral expansion of the posteroventral border of the masseteric fossa into a wide shelf is similar to *S. cegsai*, *S. gilli* and *S. maddocki*. The pterygoid fossa is more inflated posteriorly than any other *Sthenurus* species and in this respect, *S. baileyi* resembles *Procoptodon*.

Size and morphology of dp2 most resembles that of *S. brownei* but is not as narrow anteriorly relative to the posterior part of the tooth. The median valley is also narrower. Superficially, the dp2 buccal crest appears similar in length to that of *S. brownei* but this impression is created because the wear sustained has resulted in the crest becoming confluent with the small cuspules to its anterior. dp3 is also similar in size and morphology to that of *S. brownei*, but the cristid obliqua maintains contact with the hypoconid apex and there are fewer enamel crenulations on the lophid faces. In these characters, the *S. baileyi* dp^3 more closely resembles that of *S. occidentalis*.

In morphology, size relative to the molars, and orientation of the main and buccal crests, the *S. baileyi* p^3 is similar to that of *S. antiquus* (Fig. 8). It differs by being smaller, lower crowned, slightly more inflated anteriorly and having a straighter main crest orientated from the posterolingual to the anterobuccal corner of the tooth. In *S. antiquus*, the posterior part of the main crest trends anterobuccally then straightens anteriorly along the tooth's midline. The *S. baileyi* p3 shares with *S. brachyselenis* the major features of the main crest and a ridgelet traversing the median valley but is easily distinguished by its larger size, slightly greater width relative to length (ratio 0.55 compared with 0.52) and longer, straighter buccal crest (Fig. 8). In size and general outline, the *S. baileyi* p3 is also similar to *S. brownei* but is lower crowned and bears a considerably shorter buccal crest.

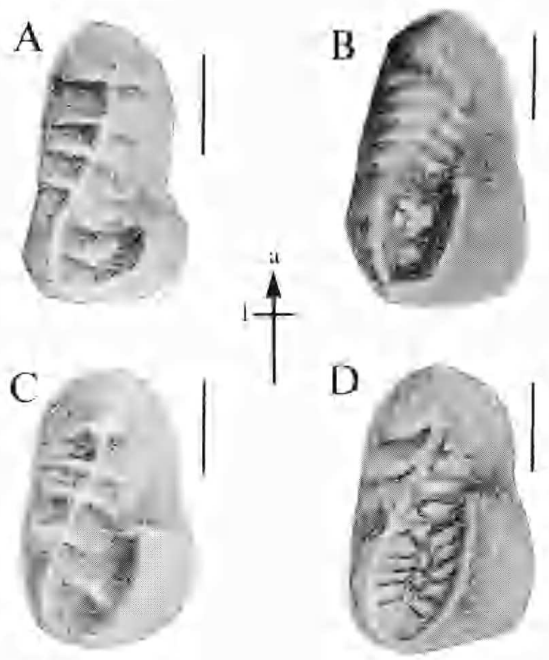

Fig. 8. Comparative sketches of right p3 in occlusal view. A. *Sthenurus brachyselenis*. B. *S. antiquus*. C. *S. baileyi* sp. nov. D. *S. brownei*. Scale bars = 5 mm. Abbrevs: a = anterior, l = lingual.

In size and crown height, the lower molars of *S. baileyi* are somewhat similar to those of *S. cegsai* and *S. antiquus*, but are most similar to those of *S. brachyselenis*. They differ from the latter in their greater width relative to length (ratio 0.84 compared with 0.72), in the anterior cingulum not being symmetrically tapered anteriorly and the shelf-like inflation on the posterior face of the hypolophid being much less pronounced. In general, *S. baileyi*, *S. brachyselenis*, *S. cegsai* and *S. antiquus* have relatively smooth lophid faces, with only a few fine enamel crenulations.

Discussion

Sthenurus baileyi sp. nov. retains a suite of craniodental characters that suggest a fairly plesiomorphic position within the genus. Although the deposits from which the species is known are Pleistocene in age, *S. baileyi* is most closely comparable with the Pliocene *S. antiquus* from Chinchilla in southeastern Queensland and *S. brachyselenis*, a species of uncertain age from Wellington Caves, eastern New South Wales. p3 is very similar to *S. antiquus*, but considerably more derived than *S. brachyselenis*, given its greater robustness relative to the molars and longer, straighter buccal crest. In *S. brachyselenis*, p3 is quite narrow and has a short, crescentic buccal crest restricted to its posterobuccal corner, features which are considered plesiomorphic for the genus (Prideaux & Wells 1997). The lower molars are intermediate between *S. brachyselenis* and *S. antiquus* in general morphology, but, unfortunately, no upper molars for the former are known. However, the upper molars of *S. baileyi* are very similar to those of *S. antiquus*. Based on a comparison of single upper molars, these two species would be difficult to separate. However, P3 is notably more derived in *S. baileyi*, the lingual cingulum having become raised into a crest subequal in height with the buccal crest. In *S. antiquus* it is markedly lower.

Although the only known cranium is incomplete, *S. baileyi* can be clearly distinguished from all species of *Sthenurus* for which the cranium is known. While exhibiting a similar degree of brachycephaly to *S. occidentalis*, *S. baileyi* possesses a shorter, broader rostrum and a less inflated frontal region than any of the other brachycephalic Pleistocene species. Increased inflation of the frontals appears to have co-evolved with increased cheek tooth complexity in the lineage (or possibly lineages) leading to the more brachycephalic (shorter-faced) species, eg. *S. brownei*, *S. occidentalis* and *S. maddocki*. The modest degree of frontal inflation, relatively simple low crowned molars and short buccal crest not joining the main crest anteriorly on p3 provide a conceivable antecedent morphology to these other species.

Unfortunately, only one ramus and one maxilla fragment of *S. antiquus* are known but given the dental similarities between this species and *S. baileyi*, the likelihood may be that these reflect overall cranial similarities. Although the dentary of *S. antiquus* is incomplete, one important difference in the cranium of this species and *S. baileyi* may be indicated by the longer cheek tooth row relative to dentary depth observed in *S. antiquus* (ratio 2.42 compared with 1.85 for *S. baileyi*). This suggests a relatively longer dentary and therefore, a more elongate cranium than for *S. baileyi*. This feature, in conjunction with the slightly higher crowned molars, and more distinct cristid obliqua and paracristid, may make *S. antiquus* a possible structural precursor to the lineage that led to the more dolichocephalic (longer-faced) Pleistocene species. This contention is supported by the fact that the lingual crest of the *S. antiquus* P3 is notably lower than the buccal crest, a feature shared by the more dolichocephalic species. In the more brachycephalic species the crests tend to be subequal in height. Since raising of the lingual cingulum into a crest is a synapomorphy for all sthenurines excluding the plesiomorphic late Miocene *Hadronomas puckridgi* Woodburne, 1967 (Fig. 9), a lower crest may be regarded as a more plesiomorphic condition.

Despite the reliance on relatively limited Pliocene material, the similarities between *S. baileyi* and *S. antiquus* imply a close relationship. They are more derived than *S. regsai* and *S. brachyselenis* but more plesiomorphic than any described Pleistocene species. Features not shared with each other are either those shared with the more dolichocephalic species in the case of *S. antiquus*, or with the more brachycephalic species in the case of *S. baileyi*. If Tedford's (1966) subgeneric (generic *sensu* Flannery 1983) definitions hold (i.e. *Simosthenurus* = brachycephalic, low-crowned cheek teeth with low links and many coarse enamel crenulations, *Sthenurus sensu stricto* = dolichocephalic, high crowned cheek teeth with strong links and few fine enamel crenulations), then *S. antiquus* may represent the least derived species in the subgenus *Sthenurus*, while *S. baileyi* may fulfil a similar position in *Simosthenurus* (Fig. 9). Because *S. notabilis* Bartholomai, 1963, an apparently derived dolichocephalic species co-occurs with *S. antiquus* in the Pliocene Chinchilla deposit, the divergence of the shorter- and longer-faced sthenurine groups must have occurred much earlier in the Pliocene. Similarly, very derived species co-occur with *S. baileyi* in the Pleistocene, but all that this demonstrates is that *S. antiquus* and *S. baileyi* are structural precursors to the dolichocephalic and brachycephalic lineages, rather than part of their direct ancestry.

So given their verisimilitude, are the differences between *S. baileyi* and *S. antiquus* sufficient to warrant placement in different subgenera? While they do not possess many of the extreme character states Tedford (1966) used to define the subgenera, the question is phylogenetically irrelevant so long as *Simosthenurus* and *Sthenurus* s.s. are monophyletic. The validity of these taxa is currently under investigation by one of us (GJP) and requires some revision, since the number of described sthenurine

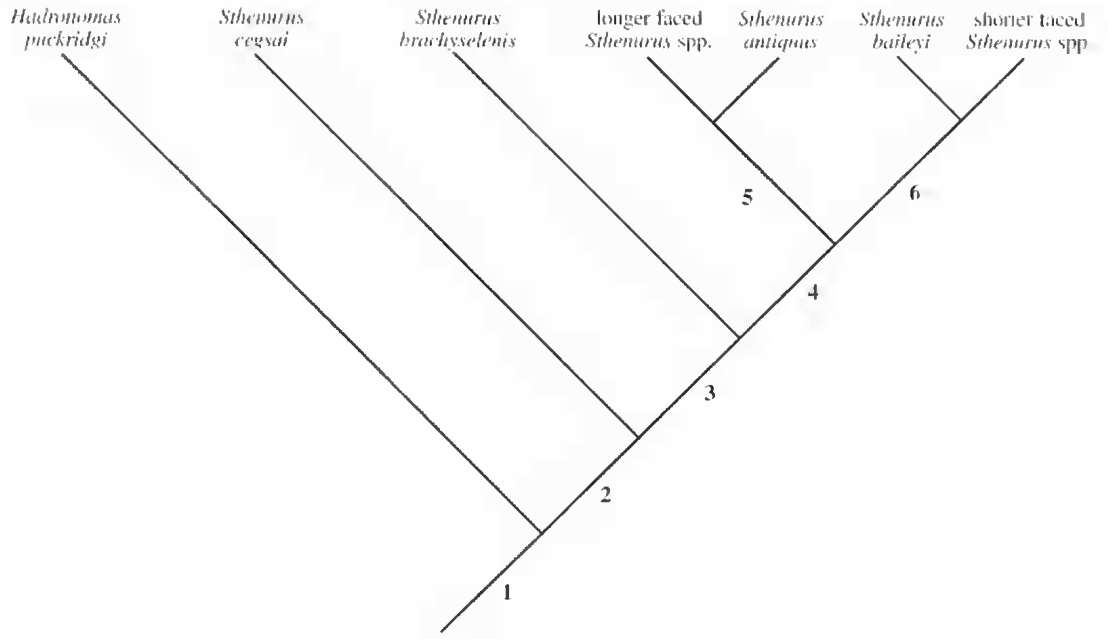

Fig. 9. Possible phylogram of basal relations in the Sthenurinae, based on the following synapomorphies. 1. Cranium relatively large; neurocranium flexed dorsally relative to rostrum; occiput close to vertical, broad and deep with well-developed lambdoid crest; large palatal vacuities, narrow post-palatine bars; deep jugal expansion forming ectoglenoid process; laterally expanded supraorbital crests; ectotympanic thick, wide, cancellous and ventrally-keeled; ascending ramus relatively vertical, with pterygoid fossa elevated and deep; digastric sulcus / eminence well-developed; I2 very small and splint-like; I3 dominated by buccal crest, lingual crest restricted to anterolingual corner; upper incisors form V-shape when viewed ventrally; C1 absent; p3 bears posterobuccal cingulum; molars fairly short relative width and squarish in occlusal view; molar lophs relatively straight and close to parallel; lower molars with posterior face of hypolophid inflated ventrally. 2. Rostrum broad and deep; zygomatic process of squamosal relatively deep; dentaries ankylosed at symphysis; mandibular ramus deep and wide, with depth at symphysis barely shallower than beneath molars; P3 with lingual cingulum raised into crest, separated from buccal or main crest by longitudinal basin traversed by ridgelets; p3 with buccal cingulum raised into crest. 3. p3 with curved buccal crest separated from main crest by wide median valley; p3 widened posteriorly; molars with more fine enamel crenulations. 4. p3 wider overall relative to length, with longer buccal crest; lower molars with cristid obliqua and paracristid shifted more lingually. 5. Cheek tooth row long relative to ramus depth, higher crowned molars, more prominent cristid obliqua and paracristid. 6. Cheek tooth row short relative to ramus depth; brachycephalic; retained lower crowned molars, low cristid obliqua and paracristid.

species has roughly doubled since Tedford's (1966) review. Almost certainly, *S. cegsai* and *S. brachyselenis* have no place within the two subgenera because they lack many of the delimiting character states and appear to be the earliest derivations from the sthenurine lineage, post-*Hadronomas puckridgi* (Fig. 9). We await the discovery of further Pliocene species to confirm exactly where *S. cegsai* and *S. brachyselenis* fit within the sthenurine radiation. As more taxa become available more light will inevitably be thrown on this paramount phase in sthenurine diversification.

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Appendix

Material used for comparison with *S. baileyi*. See "Introduction" for abbreviations, except AM = Australian Museum, QM = Queensland Museum.

Species	Registration Number	Locality
Sthenurus antiquus	QM F2931, F2973	Chinchilla, Darling Downs, Qld
S. brachyscelenis	AM F31026	Wellington Caves, NSW
S. browneí (eastern form)	SAMA P20483, FU 0202, FU 0271	Victoria Fossil Cave, Naracoorte, SA
S. cegsaí	SAMA P31800 (holotype)	Corra Lynn Cave, Curramulka, SA
S. gilli	SAMA P16528, P16629, P20797, FU 0246	Victoria Fossil Cave, Naracoorte, SA
S. maddocki	SAMA P16627, P16643, P16673	Victoria Fossil Cave, Naracoorte, SA
S. occidentalis (eastern form)	SAMA P20798, P27799	Victoria Fossil Cave, Naracoorte, SA
S. oreas	QM F2923 (holotype)	Darling Downs, Qld
S. pales	SAMA P27797	Victoria Fossil Cave, Naracoorte, SA